

SAME-SEX MOUNTING BEHAVIOR BETWEEN JUVENILES AND ADULT MALES OF THE WHITE-BEARDED MANAKIN (*MANACUS MANACUS*)

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Abstract · Adult males of lekking species compete with each other during sexual displays to attract females. Juvenile males usually are inexperienced in displays and they have minimal chances of attracting females that visit adults. Despite this supposed lack of competition between adults and juveniles, inexperienced juveniles of the White-bearded Manakin (*Manacus manacus*) that try to rehearse displays in lek areas may be chased aggressively by adult males. Here, I describe same-sex mounting behavior between *M. manacus* adults and juveniles. Two juvenile males entered the arenas of two high-ranking adults and rehearsed jump-snap display soon after they were mounted by adults. Adults did not chase the juveniles, showing no immediate competition or aggressiveness. Four years later, the same (individually-marked) juveniles had become established adults on the same lek areas where the same-sex mounting behavior was recorded. For juveniles, the same-sex mounting behavior may facilitate their approach to arenas of adults and acquisition of display experience. For adults, benefits derived from such behavior may include social hierarchy imposition and avoidance of conflicts with potentially future newcomer juvenile males in lek areas. However, alternative explanations, such as mistaking juvenile males for females by adult males, cannot be ruled out.

Resumo · O comportamento de montar entre jovens e adultos machos da rendeira (*Manacus manacus*)

Machos adultos que possuem o sistema reprodutivo de lek competem intensamente durante exibições sexuais para atrair fêmeas. Machos juvenis geralmente possuem pouca experiência em exibições e portanto, eles possuem poucas chances de atrair as fêmeas que visitam machos adultos. Apesar desta suposta falta de competição entre machos adultos e jovens, alguns jovens inexperientes de rendeiras (*Manacus manacus*) que tentam praticar exibições podem ser perseguidos por adultos agressivos. No presente estudo, eu descrevo o comportamento de montar, característico da cópula entre machos e fêmeas, entre machos adultos e machos jovens da rendeira. Dois machos jovens praticaram manobras de exibição em duas arenas de machos adultos logo depois que foram montados pelos mesmos adultos. Os adultos não perseguiram estes machos jovens, evidenciando nenhuma competição ou agressividade. Quatro anos depois, os mesmos jovens (individualmente marcados) se estabeleceram nas mesmas áreas de lek onde o comportamento de montar foi registrado. Para os jovens, o comportamento de montar pode facilitar a aproximação em arenas de adultos e a aquisição de experiência em exibições. Para os adultos, os benefícios derivados do comportamento de montar podem incluir imposição de hierarquia social sobre outros machos jovens e eliminação de futuros conflitos com potenciais machos jovens que queiram se estabelecer nas áreas de lek. Apesar dos resultados, um possível erro de identificação de sexo entre machos jovens e fêmeas por machos adultos não é descartado.

Key words: Courtship · Dominance · Interaction · Juvenile · Manakin · Pipridae · Sexual selection

INTRODUCTION

Lekking bird species often show a variety of acrobatic movements, songs, and plumage ornaments that have presumably evolved to attract the attention of females (Höglund & Alatalo 1995, Johnsgard 1994). A good example of lekking species are the Neotropical bearded manakins (*Manacus* spp., Pipridae), whose males compete intensively to copulate with females (Chapman 1935, Cestari et al. 2016). Neotropical bearded manakins are one of the best-studied groups of manakins in terms of natural history (Chapman 1935, Snow 1962, Cestari & Pizo 2012), physiology (Fusani & Schlinger 2012, Fuxjager & Schlinger 2015, Chiver & Schlinger 2017), and sexual selection (Barske et al. 2014, 2015; Cestari et al. 2016); however, little is known about the establishment of hierarchy among males in leks (Chapman 1935, Snow 1962, Shorey 2002, Cestari et al. 2016).

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Juvenile bearded manakin males are inexperienced in displays and have minimal chances of attracting females that visit adults (Chapman 1935, Snow 1962, Lill 1974). Nevertheless, juveniles may be chased away by territorial adult males when they try to rehearse their displays in the adult's display court (Snow 1962), and this remains an intriguing question once juveniles are not considered an immediate threat and do not compete with adults for matings. Here, I describe same-sex mounting behavior between intruding juveniles and resident adult males of the White-bearded Manakin (*Manacus manacus*), based on recordings and observations of behavior between 2013–2017.

METHODS

Study species. *Manacus manacus* is a small 15–18 g lekking bird with widespread geographic distribution from Colombia to northeast Argentina. This species inhabits continuous and fragmented forests of Amazon basin and Atlantic Forest of South America (Sick 1997, Snow 2004). Males have black cap, back, wing and tail, grey rump, upper tail coverts, flanks and belly, and white neck, whereas females and juvenile males are olive-green above, greyer and paler below (Snow 2004). A lek area traditionally contains 4–10 circular arenas on the forest floor. Arenas are 0.15–0.90 m diameter and may be 1–82 m apart (Cestari & Pizo 2012). Each arena is delimited by two or more saplings and typically has an adult male as owner that defends its territory from invaders (i.e., other adults and juvenile males) (Chapman 1935, Snow 1962, Lill 1974). Adult males frequently clean their arenas from debris and leaves on the forest floor (Darnton 1958, Snow 1962, Lill 1974, Uy & Endler 2004, Stein & Uy 2006).

Manacus males display fast and precise acrobatic movements to attract females. The jump-snap is one of the most impressive displays during the final pre-copulatory stage with females. During the exhibition, a male jumps from one sapling and then 'snap' his wings in the midair making a 180° horizontal loop before perching on the next sapling, then pointing his head with the beard bristled to the centre of the arena. The 'snap' is a mechanical song emitted when males flip the wings above back (Snow 1962) (Supplementary Material online, file 1). When joining the display dance, a female tests the male performance by flying milliseconds before him and thus following the direction of his jumps (Barske et al. 2015). Females observe the movements of males, but instead of jumping and snapping in midair between saplings, the females fly and make no mechanical song (Fusani et al. 2007, Chiver & Schlinger 2017). When ready to copulate, a female perches on the basal portion of the main sapling of the arena and the male slides down to the female after jumping from the ground (Snow 1962).

The juvenile plumage of *M. manacus* lasts for about one year, after which individuals molt into the

adult plumage. During the juvenile period, males look for vacated arenas in the border of lek areas or non-lek areas with abundance of saplings where they may rehearse jump-snap displays. Juvenile males practice displays alone or together with other juveniles in vacated arenas. They emit a lower mechanical song than the adult males when flipping the wings above back (the 'snip' sound). Also, their display movements are less coordinated than in adults (Snow 1962). Less frequently, they are seen displaying with adults (Supplementary Material online, file 1). Some juveniles may be chased by adult males when they try to rehearse displays in arenas (Supplementary Material online, file 2) (Snow 1962, Lill 1974).

Study area. Behavioral observations and recordings of videos of *M. manacus* were conducted at Juréia-Itatins Ecological Station in southeastern Brazil (from 24°10'S, 46°55'W to 24°33'S, 47°13'W). Climate is subtropical and humid (Holdridge 1967). Mean annual rainfall is 2278 mm with a rainy season from October to April, and dry season from May to September. Mean annual temperature is 21.4°C with maximum and minimum temperatures averaging 25.8°C and 19°C, respectively (Tarifa 2004). In this area, leks are commonly found in the lowland and the lowest mountain forests that comprise the Atlantic forest biome (Cestari & Pizo 2012).

Behavioral observations. The behavior of two resident high-ranking adult males (see Cestari et al. 2016 for detailed information about how adult males were distinguished as high-ranking or low-ranking in hierarchy) in two distinct lek areas was recorded using Go Pro® HD mini-cameras. Cameras were camouflaged with leaves and mounted up to 5 m from individual arenas. One-morning recordings (06:00–09:00 h) (BRT) of sexual behavior performed by the resident adult males and visitors (juveniles and females) were done in the two arenas on 14 and 16 September 2013, respectively. Two mist-nets were set up on trails 10 m away from the lekking arenas. Simultaneously to the camera recordings, I observed the behavior of birds from a hidden place 5 m away from both arenas and mist-nets. This position allowed me to observe the flight trajectory of birds from arena to the mist-nets and correctly identify the trapped birds. When caught in a mist net all birds were color-banded for future identifications. For two consecutive mornings on 9 and 10 January 2017, I returned to the two lek areas, in which behavior of individuals was observed in 2013, and looked for banded birds.

RESULTS

In September 2013, 10 out of 38 witnessed visits by individuals with female/juvenile-like plumage to the arenas of two high-ranking adults from different lek areas resulted in those males mounting the visitor. For two of the visitors, I could confirm in 2017 that

they were juvenile males in 2013, based on their color-markings and behavior. These juveniles approached the arenas and engaged in the duodance with adults. During the jump-snap, juvenile males flew like females (did not jump like adult males) and they occasionally produced the 'snip' sound with their wings in midair. A slow-motion video (100 frames/s) revealed more precisely the movements of one juvenile and one adult in a duo dance (Supplementary file 1). A few seconds before mounting, the juveniles perched on the basal portion of the main sapling of the arenas and allowed adult males mounted them as it typically occurs with females, i.e., the adults slid down to the direction of the juveniles after the adults jumped from the ground. Soon after they were mounted by adults, these juveniles rehearsed jump-snap displays with 'snip' and were not chased aggressively by the high-ranking males (Supplementary Material online, file 3).

In January 2017, I observed two color-banded adult males, whose color band combinations matched those of juvenile individuals that were mounted by territorial males in September 2013. They had established their own display arenas, distanced less than 5 m from the arenas belonging to the adults that mounted them in 2013. The color-banded individuals interacted with these older adults on the limit of their territories and the dominant and older males extended their beard, gave little jumps along the perch, held their head low and turned it from side to side, or raised and vibrated its wings. The older males in the lek behaved as dominants over the younger males as suggested by Snow (1962) and Shorey (2002).

DISCUSSION

My observations provide first evidence of same-sex mounting behavior in *M. manacus*. Given that such false copulations will not result in offspring sired this raises the question of why they occur. A non-adaptive explanation is that same-sex mounting could happen due to adult males mistaking juvenile males for females. Alternatively, same-sex mounting behavior could be adaptive if it represents a way for adult males to display their dominance status, and helps to mediate male-male interactions or even the formation of male-male coalitions.

Same-sex mounting behavior between males is more prevalent in polygamous mating systems, such as in lekking species (Bagemihl 1999; MacFarlane et al. 2007, 2010) like *M. manacus*. These species are characterized by the complete lack of male care for offspring, and in such species males may be less selective in their mate choice, given that there are no strong costs of mistaken mating (such as same-sex mounting). The possibility of mistakes is increased in this case since juvenile males look similar to females. It has been hypothesized that delayed plumage maturation in juveniles and similarity in plumage with

females have evolved to reduce aggression from adult males (Foster 1987, McDonald 1989, DuVal 2005). On the other hand, other researchers doubt that males do not have the ability to distinguish juvenile males from females (Chapman 1935, Snow 1962, McDonald 1993). Indeed, recent work reveals that juvenile male plumage in *M. manacus* differs from female plumage in the UV reflectance (Morales-Betancourt & Castaño-Villa 2017), which should be visible to birds but invisible to humans (Eaton 2005, Burns & Shultz 2012). In addition, juvenile males generally are noisier than females; these males perform uncoordinated jump-snap displays during flights in or outside lek areas, while females usually participate of displays in silence and only inside arenas (Snow 1962, Barske et al. 2015).

Manacus males reach complete maturity (i.e., molt to adult plumage) after their first year of life, and the degree of threat or aggressive behavior between males probably varies with age, display experience, and male hierarchical position of dominance. During a great part of the juvenile phase, *Manacus* males are not mature or experienced enough to attract mates (Snow 1962). In this time, a subordinate behavior, such as allowing same-sex mounting behavior, may facilitate the approach of juveniles to arenas of competitive adults and acquire experience on display behavior at the lek (see Collis & Borgia 1993). Alternatively, same-sex mounting may be an adaptive behavior if it mediates male-male interactions with more dominant (i.e., high-ranking) males in a lek area, thus avoiding future aggressive conflicts (Fujioka & Yamagishi 1981, Poiani 2008). Males may chase each other and fight severely during territory invasions (Snow 1962). Benefits to dominant males derived from same-sex behavior include social hierarchy imposition and avoidance of conflicts with potentially future newcomer males in the lek area. Furthermore, ritualized behavior among *M. manacus* males in lek areas as described in the present study evidences a high degree of social hierarchy (Snow 1962, Shorey 2002). Dominance hierarchy in *Manacus* spp. may optimize energy and time use to focus on sexual display and avoid disruptions by competing males (Snow 1962, Lill 1974).

The establishment of two of the visiting juveniles in the same lek areas where the same-sexual behavior with adults was recorded suggests that the establishment of dominance hierarchy in *Manacus* spp. may initiate early during the juvenile phase. After becoming established in a lek area, a newcomer male may rise in hierarchy with age and, according to social interactions with other males, may become more experienced in sexual skills to attract females, and in aggressive behavior against invaders (Snow 1962, Lill 1974). Dominance hierarchies occur among males of manakin species, such as Long-tailed Manakin (*Chiroxiphia linearis*) and Swallow-tailed Manakin (*C. caudata*). These species have hierarchy among males to attract females in a queued system. The dominant males are often successful in mating, and low-ranking

males take a long time (i.e., four and two years, respectively) to reach complete sexual maturity and to ascend in hierarchy according to their sexual and social skills (Foster 1981, McDonald 1993).

I encourage more observations to disentangle the potential explanations of same-sex mounting behavior in *M. manacus*.

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REFERENCES

- Bagemihl, B (1999) *Biological exuberance. Animal homosexuality and natural diversity*. Profile Books Ltd., London, UK.
- Barske, J, L Fusani, M Wikelski, NY Feng, M Santos & BA Schlinger (2014) Energetics of the acrobatic courtship in male Golden-collared Manakins (*Manacus vitellinus*). *Proceedings of the Royal Society of London B* 281: 2013–2482.
- Barske, J, BA Schlinger & L Fusani (2015) The presence of female influences courtship performance of male manakins. *The Auk* 132: 594–603.
- Burns, KJ & AJ Shultz (2012) Widespread cryptic dichromatism and ultraviolet reflectance in the largest radiation of Neotropical songbirds: implications of accounting for avian vision in the study of plumage evolution. *The Auk* 129: 211–221.
- Cestari, C & MA Pizo (2012) Lek phenology of White-bearded Manakin (*Manacus manacus*, Aves: Passeriformes: Pipridae) in a subtropical region. *Journal of Natural History* 46: 2999–3009.
- Cestari, C, Loisele BA & MA Pizo (2016) Trade-offs in male display activity with lek size. *PloS One* 11: e0162943.
- Chapman, FM (1935) The courtship of Gould's Manakin (*Manacus vitellinus vitellinus*) on Barro Colorado Island, Canal Zone. *Bulletin of American Museum of Natural History* 68: 471–525.
- Chiver, I & BA Schlinger (2017) Sex differences in androgen activation of complex courtship behaviour. *Animal Behaviour* 124: 109–117.
- Darnton, I (1958) The display of the manakin *Manacus manacus*. *Ibis* 100: 52–58.
- Collis, K & G Borgia (1993) The costs of male display and delayed plumage maturation in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *Ethology* 94: 59–71.
- DuVal, E (2005) Age-based plumage changes in the Lance-tailed Manakin: a two year delay in plumage maturation. *The Condor* 107: 915–920.
- Eaton, MD (2005) Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *Proceedings of National Academic of Science USA* 31: 10942–10946.
- Foster, MS (1981) Cooperative behaviour and social organization of the Swallow-tailed Manakin (*Chiroxiphia caudata*). *Behavioral Ecology Sociobiology* 9: 167–177.
- Foster, MS (1987) Delayed maturation, neoteny and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* 41: 547–558.
- Fujioka, M & S Yamagishi (1981) Extramarital and pair copulations in the Cattle Egret. *The Auk* 98: 134–144.
- Fusani, L, M Giordano, LB Day & BA Schlinger (2007) High-speed video analysis reveals individual variability in the courtship displays of male Golden-collared Manakins. *Ethology* 113: 964–972.
- Fusani, L & BA Schlinger (2012) Proximate and ultimate causes of male courtship behavior in Golden-collared Manakin. *Journal of Ornithology* 153: S119–S124.
- Fuxjager, MJ & BA Schlinger (2015) Perspectives on the evolution of animal dancing: a case study of manakins. *Behavioral Sciences* 6: 7–12.
- Höglund, J & RV Alatalo (1995) *Leks*. Princeton University Press, Princeton, New Jersey, USA.
- Holdridge, LR (1967) *Life zone ecology*. Tropical Science Center, San Jose, Costa Rica.
- Johnsgard, PA (1994) *Arena birds. Sexual selection and behaviour*. Smithsonian Institution Press, Washington, DC, USA.
- Lill, A (1974) Sexual behaviour of the lek-forming White-bearded Manakin (*Manacus manacus trinitatis* Hartert). *Zeitschrift für Tierpsychologie* 36: 1–36.
- MacFarlane, GR, SP Blomberg, G Kaplan & LJ Rogers (2007) Same-sex sexual behaviour in birds: expression is related to social mating system and state of development at hatching. *Behavioral Ecology* 18: 21–33.
- MacFarlane, GR, SP Blomberg & PL Vasey (2010) Homosexual behaviour in birds: frequency of expression is related to parental care disparity between the sexes. *Animal Behaviour* 80: 375–390.
- McDonald, DB (1989) Cooperation under sexual selection: age-graded changes in a lekking bird. *The American Naturalist* 134: 709–730.
- McDonald, DB (1993) Delayed plumage maturation and orderly queues for status - a manakin mannequin experiment. *Ethology* 94: 31–45.
- Morales-Betancourt, JA & GJ Castaño-Villa (2017) Males in seemingly female-like plumage do not mimic females: UV reflectance reveals temporal cryptic dimorphism in a manakin species exhibiting delayed plumage maturation. *Journal of Avian Biology*: doi:10.1111/jav.01467.
- Poiani, A (2008) Same-sex mounting in birds: comparative test of a synthetic reproductive skew model of homosexuality. *Open Ornithology Journal* 1: 36–45.
- Shorey, L (2002) Mating success on White-bearded Manakin (*Manacus manacus*) leks: male characteristics and relatedness. *Behavioral Ecology and Sociobiology* 52: 451–457.
- Sick, H (1997) *Ornitologia Brasileira*. Nova Fronteira, Rio de Janeiro, Brazil.
- Snow, DW (1962) A field study of the Black-and-white Manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47: 65–104.
- Snow, DW (2004) Family Pipridae (Manakins). Pp 110–169 in del Hoyo, J, A Elliott & DA Christie (eds). *Handbook of the birds of the world. Volume 9: Cotingas to pipits and wag-tails*. Lynx Edicions, Barcelona, Spain.
- Stein, AC & JAC Uy (2006) Plumage brightness predicts male mating success in the lekking Golden-collared Manakin, *Manacus vitellinus*. *Behavioral Ecology* 17: 41–47.
- Tarifa, JR (2004) Unidades climáticas dos maciços litorâneos da Juréia-Itatins. Pp 42–50 in Marques, OAV & W Duleba (eds). *Estação Ecológica Juréia-Itatins: ambiente físico, flora e fauna*. Holos, Ribeirão Preto, Brazil.
- Uy, JAC & JA Endler (2004) Modification of the visual background increases the conspicuousness of Golden-collared Manakin displays. *Behavioral Ecology* 15: 1003–1010.